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Towards the identification of Conservation Units in Atlantic salmon from Eastern Canada

Pour une délimitation des unités de conservation du saumon atlantique dans l'est du Canada

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ABSTRACT

Atlantic salmon *(Salmo salar)* is the only naturally occurring (non-introduced) representative of it's genus in Eastern Canada. During the freshwater phase of it's life cycle, the species once occupied most rivers and major streams along the Atlantic coasts of New Brunswick, Nova Scotia, Prince Edward Island, Quebec, and Newfoundland, and from the Maine-New Brunswick border in the south to Ungava Bay in the north. Within this extensive geographic distribution are several large regional zones that vary in terms of topographic relief, landforms, soils, water features, vegetation and climate. Riparian habitat also varies within these zones, with neighbouring rivers differing in terms of stream gradient, maximum distance to river mouth, bedrock type, pH, temperature, predators, and prey availability. Phenotypic differences have been identified among salmon from different general locations and between salmon from neighbouring rivers. In some instances, variation observed may reflect environmentally induced phenotypic plasticity, but in others, possible adaptations to local conditions. Overall, however, little is known about the existence and distribution of genetically based differences in life history and morphological traits among Atlantic salmon from Eastern Canada, and even less about the adaptive significance of such differences.

Analyses of neutral molecular genetic markers can help elucidate patterns and extent of genetic structuring, and provide insight into the amount of gene flow among salmon from different locations; this information is useful in assessing the potential for adaptive differences to accrue and can assist in identifying major ancestral lineages of Atlantic salmon. Although several published studies of neutral molecular genetic variation have been carried out that include populations of Atlantic salmon from Eastern Canada, most involve only one or two rivers from a few regions, and are of limited scope and utility in resolving biodiversity for conservation purposes. However, one broad-scale analysis of multiple allozyme loci has been completed, and fine-scale coverage of the Maritimes is also available for several classes of molecular genetic markers.

A number of methods have been developed to categorize within-species biodiversity for conservation purposes. Many of these involve similar approaches and utilize largely overlapping suites of information in delineating Conservation Units (CUs), defined here as "groups of individuals likely exhibiting unique adaptations that are largely reproductively isolated from other groups, and that may represent an important component of a species' biodiversity". In other instances, however, alternate methods employ different types of information, or use the same or similar information in different ways, possibly resulting in very different outcomes. Here, I make a case for testing candidate groupings against several divergent alternative methods in order to maximize the identification of biodiversity in Atlantic salmon from Eastern Canada.

RÉSUMÉ

La saumon atlantique *(Salmo salar)* est la seule espèce de son genre qui soit naturellement présente (non introduite) dans l'est du Canada. Au cours de la phase d'eau douce de son cycle biologique, l'espèce a déjà occupé la plupart des cours d'eau de la côte atlantique du Nouveau-Brunswick, de la Nouvelle-Écosse, de l'île-du-Prince-Édouard, de l'Ontario, du Québec et de Terre-Neuve, à partir de la frontière du Maine et du Nouveau-Brunswick dans le sud jusqu'à la baie d'Ungava au nord. Cette vaste aire de répartition comporte plusieurs grandes zones régionales aux caractéristiques variables sur les plans du relief, des sols, des détails hydrographiques, de la végétation et du climat. L'habitat varie également dans ces zones, les cours d'eau avoisinants affichant aussi des différences quant au gradient, à la distance maximale jusqu'à l'embouchure, au substrat rocheux, au pH, à la température, aux prédateurs, à la disponibilité des proies, etc. Certaines différences phénotypiques ont été observées chez les saumons de différents endroits et parmi les saumons de cours d'eau avoisinants, probablement en réaction aux différents milieux d'eau douce occupés par les jeunes. Dans certains cas, les différences peuvent correspondre à la plasticité phénotypique induite par le milieu, mais dans d'autres, les variations observées représenteraient une adaptation à des conditions locales. Dans l'ensemble, cependant, on connaît peu de choses sur l'existence et la répartition des différences d'origine génétique dans le cycle biologique et les traits morphologiques du saumon atlantique de l'est du Canada, et encore moins à propos de l'importance des différences observées sur le plan de l'adaptation.

L'analyse des marqueurs génétiques moléculaires neutres peut aider à élucider les tendances et l'étendue de la structure génétique, et peut contribuer à mesurer la quantité d'échanges de gènes entre saumons de différents endroits; cette information est utile pour évaluer le potentiel cumulatif des différences adaptatives et peut servir à déterminer le lignage des saumons. Bien que plusieurs études publiées aient été menées sur les variations génétiques moléculaires neutres notamment de populations de saumon atlantique de l'est du Canada, la plupart d'entre elles portent uniquement sur un ou deux cours d'eau de quelques régions et elles ont une portée et une utilité limitées pour ce qui est de résoudre les questions de biodiversité aux fins de la conservation. Toutefois, une analyse à grande échelle de multiples loci d'alloenzymes a été réalisée et il existe aussi une couverture à petite échelle des Maritimes pour plusieurs catégories de marqueurs moléculaires.

Un certain nombre de méthodes ont été mises au point pour catégoriser la biodiversité au sein des espèces aux fins de la conservation. Bon nombre d'entre elles comportent des démarches semblables et font appel à des séries de données qui se recoupent largement pour délimiter les unités de conservation (CU), définies dans le présent document comme des « groupes d'individus susceptibles d'afficher des caractéristiques d'adaptation uniques, qui sont largement isolés des autres groupes sur le plan de la reproduction et qui peuvent représenter une composante importante de la biodiversité d'une espèce ». Dans d'autres cas, toutefois, d'autres méthodes ont recours à différents types d'information ou utilisent la même information ou une information semblable de différentes façons, avec des résultats vraisemblablement très différents. Ici, nous recommandons une méthode précise commune pour tenter de déterminer les UC, mais nous établissons aussi le bien-fondé de l'évaluation des groupes candidats à l'aide de plusieurs méthodes différentes afin de maximiser la détermination de la biodiversité du saumon atlantique de l'est du Canada.

INTRODUCTION

As wild anadromous Atlantic salmon throughout the lower half of the species' distribution in Canada continue to decline, the identification and categorization of remaining biodiversity is becoming increasingly urgent. In some areas, salmon have been extirpated from the majority of rivers, and it is now too late for any analyses of within- and among-population variation in molecular genetic, morphologic, meristic, behaviour, or life history traits. In other areas, the number of remaining populations are already too few to carry out comparative studies of Q_{ST} (a measure of the degree of quantitative trait differentiation among populations) and F_{ST} (a measure of the degree of differentiation at neutral molecular genetic markers); such analyses could have provided valuable insight into the basis of among-population variation in quantitative traits, and the relative role of drift versus directional selection (O'Hara and Merila, 2005). In many rivers where populations persist, there is now an insufficient number of returning adults (in the low dozens) for credible estimates of genetic differentiation and historic gene flow based on data from variable neutral molecular markers (Ruzzante, 1998; B-Rao, 2001; Kalinowski, 2005). With each passing generation that remaining populations persist at these low levels, rapid contemporaneous drift further distorts patterns of molecular genetic variation originally produced by hundreds to thousands of years of natural evolutionary processes. Finally, salmon in some persisting populations are being maintained under semi-captive conditions, and are therefore likely adapting to hatchery environments, compromising future studies of the magnitude and basis of morphologic and life history differences among remaining river populations of salmon. Clearly, the window of opportunity for assessing and categorizing original levels and patterns of biodiversity in Eastern Canada is rapidly closing.

The identification and categorization of within-species biodiversity can contribute to the conservation of remaining Atlantic Salmon in Canada in several important ways. Within the federal Species At Risk Act (SARA) there exist provisions for allowing status designation (Endangered, Threatened, and Vulnerable) for groups of individuals below the species level:

> "Wildlife species means a species, subspecies, variety of geographically or genetically distinct population of animal, plant or other organism, other than a bacteria or virus, that is wild by nature and (a) native to Canada or (b) has extended its range into Canada without human intervention and has been present in Canada for at least 50 years"

The act also prohibits the causing of direct harm (hunting, capture, harassment) to all species listed as Endangered under SARA, and includes additional restrictions on human activities intended to prevent their further decline. Geographically or genetically distinct groups of individuals, at risk of extirpation, may thus be afforded some level of protection from human disturbances.

The identification of within-species biodiversity is also important for the development and implementation of conservation programs, such as those currently underway for declining Atlantic salmon populations in Maine USA (NMFS and USFWS, 2005), Norway and Maritimes Canada (O'Reilly and Doyle, 2007). First, delineation of within- and among-population biodiversity can help prioritize scarce conservation funding so as to maximize retention of biodiversity (Weitzman, 1992; Petit *et al.*,1998; Caballero and Toro, 2002). Second, where captive breeding and rearing are involved, as in the above three examples, information on the existence of possible ancestral lineages, boundaries between reproductively isolated groups of individuals, and the presence of genetically based differences in morphology, behaviour, or life history traits that could effect fitness can be useful in minimizing outbreeding depression in future generations of Atlantic salmon. Third, identification of possible ancestral lineages, and

knowledge about of the geographic scale of local adaptation, may assist in evaluating the risk of translocating Atlantic salmon from one site to another, both for aquaculture and possible future stocking enhancement purposes (Johnson, 2000). Furthermore, an accounting of present-day phenotypic and genetic variation will be necessary for future assessments of the magnitude of loss, and rate of decline, of biodiversity in Canada. This information will be important in educating future Canadians as to the plight of local and global biodiversity, which may impact decision makers of the day and the prioritization of biological conservation relative to other competing concerns.

Although most will agree that the categorization of within-species biodiversity is imperative for effective conservation, there exists considerable debate as to how to go about identifying and classifying important biological variation. Many of the existing published approaches for delineating units for conservation, discussed in later sections of this document, are ultimately concerned with adaptive genetic variation. Here, a trait difference is said to be adaptive if it has a genetic basis (is largely heritable), and increases the survival or reproductive success of individuals with the given variant over those lacking it (Barker and Thomas, 1987; Taylor, 1991). This focus on adaptive genetic variation reflects the acknowledgement of its importance in contributing to the future evolutionary potential and probability of persistence of a population or species.

Categorizing and summarizing adaptive genetic variation within a species is complicated by the difficulty in demonstrating conclusively that observed phenotypic differences are indeed adaptive. First, heritability estimates of mostly economically important trait differences have only been carried out under laboratory conditions, not in the wild, and there are reasons to believe that findings of the former may not be transferable to the latter. Also, few studies have rigorously assessed whether a given observable trait confers a survival or reproductive advantage in the wild over another variant, or whether Atlantic salmon from a given river or tributary are more fit in their own native environment than are non-local individuals from another drainage. Studies involving the reciprocal translocation of individuals, and assessment of survival and reproductive success of both genotypes in the two environments, have not been carried out in this species at all. There is, however, a great body of circumstantial evidence for local adaptation in Atlantic salmon, summarized by Taylor (1991) and more recently by Garcia de Leaniz *et al.* (2007a,b). Unfortunately, most of this research will not be directly relevant here, as the bulk of studies discussed in these reviews involve either Pacific salmon from North America, or Atlantic salmon from rivers in Europe. Saunders (1981), in a review of environmental and genetic influences on stock-specific traits in Atlantic salmon from the Atlantic provinces and New England, USA, similarly noted that "In comparison with the abundant data reviewed by Ricker (1972) for Pacific salmonid stocks, there is a scarcity of such data for North American Atlantic salmon."

The likelihood of adaptive differences existing among populations can also be indirectly assessed by investigating the evolutionary forces responsible for the development of possible adaptive differences, namely drift, gene flow, selection, and mutation. Selection and gene flow are particularly important, with some forms of selection serving to increase the likelihood of adaptive differences developing between populations, while higher levels of historic and recent gene flow would likely serve to reduce the probability of adaptive differences developing and/or persisting through to the present. Information on the nature and magnitude of environmental differences among populations can provide insight into the existence and magnitude of differential selective pressures, while analyses of neutral molecular genetic marker variation can provide insight into the extent of historic and recent gene flow.

Here, I first describe external morphological characteristics and the general taxonomy of the species to provide a broader context for assessing the importance of Atlantic salmon biodiversity in Canada. Some discussion is also given to existing controversies on phylogenetic relationships of species within the family Salmonidae. Next I review the distribution of Atlantic salmon in North America, and the variable landscapes occupied by populations across this portion of their range, paying particular attention to features sometimes associated with observed phenotypic differences. I then discuss what little is known about phenotypic differences among populations from Eastern Canada, and evidence for the adaptive significance of this variability. As little has been done to address whether observed phenotypic differences among Atlantic salmon populations from Eastern Canada may be heritable and adaptive, I also provide some summary information from a recent global review of adaptation in Atlantic salmon (Appendix I) in the hopes that inferences can be made by which to evaluate the possible importance of observed phenotypic differences in Eastern Canada. Next, I review studies of presumably neutral molecular genetic variation among Atlantic salmon from Eastern Canada, and what they suggest about reproductive isolation and genetic structuring. This is information that goes to assessing the potential for adaptive differences to accrue, but that also may be useful in identifying major underlying ancestral lineages of Atlantic salmon in Canada. I then review the methods for identifying conservation units, including advantages and disadvantages of each.

The ultimate objective of this document is not to identify conservation units among Atlantic salmon from eastern Canada *per se*, as this will be done on a region-by-region basis, but rather to get the ball rolling by 1) providing some discussion on what is (and is not) known about adaptive genetic variation among anadromous Atlantic salmon from Eastern Canada, 2) summarizing molecular genetic variation in Eastern Atlantic salmon, and 3) recommending an overall approach for identifying CUs in this surprisingly data-poor group of populations from Eastern Canada.

NAME AND CLASSIFICATION

Most commonly referred to as Atlantic salmon, the species is also called Kennebec salmon, Sebago salmon, or Black salmon by some. The Latin or scientific name, *Salmo salar*, was given by Carolus Linneaus in 1758, and means "The Leaper", which refers to the species' ability to jump water falls several metres in height while ascending rivers prior to spawning.

Atlantic salmon are well-known members of the family Salmonidae, one of two families in the order Salmoniformes, which include Pacific salmonids, trout, chars and whitefishes. Members of the family are either freshwater or anadromous, but never entirely marine.

Taxonomic classification of Atlantic salmon

Phylum: Chordata
Class: Osteichthyes (bony fishes)
Order: Salmoniformes
Family Salmonidae (Salmon and trout)
Subfamily Salmoninae
Species: *Salmo salar* Linneaus

Within the family Salmonidae, the phylogenetic relationships among the major genera

are not fully resolved, in that analyses based on morphological characters have yielded very different tree topologies with the exception of the genus *Thymallus,* which tends to group separately from all other genera in most analyses. *Salmo* and *Oncorhynchus* (Pacific salmonids and trouts), for example, are sibling genera in morphology-based phylogenetic analyses conducted by Norden (1961), Kendall and Behnke (1984) and Dorofeyeva (1989). However, in Stearley and Smith's (1993) analysis of morphological characters, and Oakley and Phillip's (1999) review of existing molecular genetic information, including their own data from growth hormone introns, *Salmo* and *Oncorhynchus* are not sister taxa. An interesting implication of this later phylogeny is that anadromy may have evolved independently at least twice in this family. See Kinnison and Hendry (2004) for a recent, more detailed review on the phylogeny of salmon and their congeners.

The genus *Salmo* is quite large, containing approximately 30 species world-wide. Atlantic salmon *(Salmo salar)* is the only naturally occurring representative in Canada; Brown trout *(S. trutta),* though present, is an exotic species, introduced into North America in 1883. Where the two species overlap, they can be distinguished by a number of physical characteristics (Leim and Scott, 1966).

Previously, freshwater populations were thought to be taxonomically distinct from anadromous populations, and in some cases were given subspecies status, for example, Lake Saint John salmon of Quebec *(Salmo salar ouananiche)* and Sebago Lake salmon of Maine *(Salmo salar sebago)* (Scott and Scott, 1988). Systematic studies by Wilder (1947) (cited in Scott and Scott, 1988) failed to support these subspecific designations. In fact, most do not recognize any subspecies designations within Atlantic salmon, though molecular genetic studies have found European and North American salmon to be highly divergent, and Baltic sea salmon to be very distinct from remaining European salmon elsewhere (discussed below; Stahl, 1987, Bermingham *et al.*, 1991; Bourke *et al.*, 1997, Verspoor *et al.*, 1999; Nilsson *et al.*, 2001).

MORPHOLOGICAL DESCRIPTION OF SPECIES

Atlantic salmon adults are typically trout-like in shape, with elongated or fusiform bodies that are somewhat laterally compressed. The caudal peduncle is slender, and the dorsal fin fairly large and very slightly forked. A fleshy adipose fin is present anterior to the caudal peduncle. The maximum depth of the body occurs just anterior to the midpoint of the fish along the longitudinal axis, below or just posterior to the dorsal fin. The body depth is 20-23% of the total length (Scott and Crossman, 1973). The mouth is terminal, and the maxillary extends below or just posterior to the eyes. Principal dorsal rays number 10-12, principal anal rays 8-11, pelvic rays 9-10, and pectoral rays 14-15 (Scott and Crossman, 1973). While at sea, the adults are typically silver on the sides, white on the bottom, and green, blue or brown on the top, with numerous small, often X-shaped dark spots on their heads and upper half of their bodies. As they move into freshwater and prepare to spawn, adults take on a more bronze or brown colour, particularly the males, with red spots on the head and body. A small kype (turning up of the lower jaw) forms in the female and a much larger kype and general expansion of the jaws occur in the males.

Juveniles are more slender than adults and exhibit 8-11 dorso-ventrally elongated marks on both sides of their body throughout much of their residence in freshwater. Prior to their ocean migration, however, these marks are lost and the fish takes on the more silvery appearance of the adults.

BIOGEOGRAPHY AND EVIDENCE FOR LOCAL ADAPTATION AMONG ATLANTIC SALMON FROM EASTERN CANADA

Throughout part of their life history, anadromous Atlantic salmon in Canada occupy rivers and streams along the Atlantic coast, from the Maine-New Brunswick border north to Labrador and on into Ungava Bay (Parrish *et al.*, 1998). In total, the species' freshwater range in Canada spans some 36,000 kilometres of coastline, covering 15 degrees of latitude, and five ecozones, which vary in terms of climate, photoperiod, underlying bedrock, land forms, and major flora and fauna assemblages (Selby and Santry, 1996). Within these various ecozones, rivers and streams may vary greatly in terms of gradient, prey abundance, predators, temperature and other characteristics. Within rivers, too, environments may vary in terms of proximity to river mouth, temperature, and gradient. Of the many characteristics that may differ across the range of Atlantic salmon in North America, water temperature, photoperiod, and stream morphology (and related variables) are likely to be among the most important in contributing to local selective pressures, but other key selective agents include marine migration distance, mate choice and predation risk (Garcia de Leaniz *et al.* 2007a,b). The relatively stable nature of the former variables is also expected to favour the development of local adaptations in Atlantic salmon (Garcia de Leaniz *et al.* 2007b). See Table 6 of Garcia de Leaniz *et al.* (2007b) for a more comprehensive list of environmental variables for which there is some evidence of importance as presumed agents of selection.

Two comprehensive analyses of meristic and morphometic variation have been carried out on Atlantic salmon from Eastern Canada that includes multiple samples from several regions (Claytor and MacCrimmon, 1988; Claytor *et al.*, 1991). Considerable overlap in meristic characteristics was observed among rivers surveyed, and several characteristics correlated with latitude, longitude, and April-May temperatures, with the latter being the most important factor (Claytor *et al.*, 1991). Patterns of meristic variation observed, and laboratory studies from elsewhere, led the authors to conclude that the meristic traits surveyed were environmentally induced, and did not represent important genetically based adaptations. Certain morphological traits, including head length, body width, and body depth, were also found to vary among samples surveyed from Eastern Canada; populations from Newfoundland-Labrador and Gaspe-Maritime locations grouped into two distinct regional stocks based on these characteristics (Claytor and MacCrimmon, 1988). Correlations between these morphological traits and stream gradient, and findings by Riddell and Leggett (1981) of 1) a large genetic component to these same morphological trait differences and 2) evidence of an adaptive basis for these same differences, in the two populations surveyed, suggest an adaptive basis to much of the broad-scale morphological variation reported by Claytor and MacCrimmon (1988) and Claytor *et al.* (1991).

Several analyses involving multiple populations of Atlantic salmon from Eastern Canada have also provide evidence for the existence of molecular genetic adaptations. In a large-scale study of variation at the Me-2 or malic acid enzyme locus, Verspoor and Jordan (1989) noted a south-to-north cline in the frequency of certain alleles in both North American and European salmon. A similar cline in allele frequencies within individual drainages from the river mouth to the cooler headwaters was also noted, and suggests that clinal variation seen at both scales may be an adaptation to temperature in this species (Verspoor and Jordan, 1989). A north-to-south cline was also noted in levels of diversity at the Major Histocompatiblity class II (MHC II) locus in Atlantic salmon surveyed from 34 rivers from Eastern Canada (Dionne *et al.* 2007). Other observations, including 1) greater clinal variation for MHC amino acids of the peptidebinding region (the site that recognizes and binds to pathogen anitgens) and 2) the

observation that bacterial diversity increases with temperature in the rivers surveyed, suggest that variation observed may be an adaptation to bacterial diversity in these drainages (Dionne *et al.* 2007).

Atlantic salmon from Eastern Canada may also exhibit one or more important broad-scale adaptations to their marine environment. Ritter (1975) transferred hatchery-reared smolts, produced by spawning wild salmon returning to native rivers of the Northumberland Strait, into increasingly distant Maritime rivers. Rates of return to rivers within tens of kilometres of their natal streams were similar to rates for hatchery smolts released into natal streams, but return rates decreased markedly as a function of increasing geographic distance beyond a translocation distance of tens of kilometres. These results indicate the possibility of genetically based differences in marine migration routes on moderate to large geographic scales (Ritter, 1975) or some other trait related to marine survival; similar findings were reported by Reisenbichler (1988) and Altukhov and Salmenkova (1987) for coho (*Oncorhynchus kisutch)* and chum salmon, respectively.

Clearly, Atlantic salmon in Canada occupy a wide range of habitats and environments, and there is some evidence for an association between studies of molecular and phenotypic variation and environmental differences on small and large geographic scales. Populations may also vary with respect to the presence of major underlying lineages of salmon, reflecting post-Pleistocene colonization from genetically divergent salmon from different nearby refugia (for example, see Verspoor *et al.*, 2002). Given the (1) geographically extensive and variable nature of the species' freshwater environment in Canada, (2) relative geographic isolation of rivers and remarkable homing precision of salmon to spawning sites of origin, (3) presence and distribution of different ancestral lineages of Atlantic salmon in Eastern Canada, and (4) evidence in the literature for the presence of local adaptation in salmonids in general (reviewed by Taylor, 1991; Garcia de Leaniz *et al.*, 2007a,b; see also Appendix I), it would seem likely that considerable adaptive variation exists among Atlantic salmon from Eastern Canada at varying spatial scales. Finally, there may also exist distinct salmon populations occupying the same location or environment, reproductively isolated largely or entirely by timing or behaviour (sympatry). One of the best-known examples in the salmonid literature is the presence of highly genetically divergent even-odd-year pink salmon runs in rivers from the Pacific Northwest, though examples of reproductively isolated populations inhabiting the same location also exist in Atlantic salmon (Potvin and Bernatchez, 2001). Identification of conservation units must consider all levels of Atlantic salmon biodiversity if the species as a whole is to be adequately protected in Canada.

POPULATION STRUCTURING AMONG ANADROMOUS ATLANTIC SALMON

Phenotypic and parasite differences between North American and European salmon

The most obvious discontinuity in the freshwater geographic distribution of Atlantic salmon lies between Europe and North America, where thousands of kilometres of ocean or largely uninhabitable island coastline separate salmon populations from the two continents. During the marine phase of their life cycle, however, many salmon from Europe and North America migrate to feeding areas off Greenland, where they mix and are often caught together in high-seas fisheries (Reddin *et al.*, 1988; ICES, 2004). Management-related concerns associated with this fishery have precipitated research into discriminating European and North American-origin salmon caught off Greenland.

Early research by Nyman and Pippy (1972) indicated that North American and European salmon differed in terms of mean river age and mean fork length; European salmon usually smoltify after two years in freshwater versus two or three years for North American salmon, and are, on average, several centimetres longer, though considerable variation exists within both continents. Nyman and Pippy (1972) also reported differences in the abundance and incidence of occurrence of two parasites, *Anisakis simplex* and *Eubothrium crassum*, respectively, in salmon from the two continents. Extensive research into the use of scale pattern variation and discriminant function analysis (reviewed in Reddin and Friedland, 1999) has shown that European and North American salmon also differ in terms of scale growth ring patterns.

Molecular genetic differences between North American and European salmon

Nyman (1966) and Nyman and Pippy (1972) provided some of the first evidence of a biochemical distinction between European and North American salmon, demonstrating consistent differences in electropherograms of serum proteins and liver esterases. Stahl (1987) later reported deep divisions between North American and European salmon through enzyme electrophoresis. Allozyme differences between salmon from the two continents were also reported by Bourke *et al.* (1997) and Verspoor and McCarthy (1997). In fact, extensive genomic divergence between North American and European salmon can be inferred by the observation that substantial allele frequency differences have been found repeatedly at multiple classes of genetic markers surveyed, including allozymes, as stated above, but also nuclear rRNA genes (Cutler *et al.*, 1991), minisatellite DNA (Taggart *et al.*, 1995), microsatellite DNA (McConnell *et al.*, 1995; King *et al.*, 2001; Gilbey *et al.*, 2005), and mitochondrial DNA (Bermingham *et al.*, 1991; Birt *et al.*, 1991; Kauppi *et al.*, (1997); King *et al.*, 2000; Nilsson *et al.*, 2001; Asplund *et al.*, 2004; Gilbey *et al.*, 2005). The magnitude of difference observed between mitochondrial DNA types commonly found in European and North American Atlantic salmon, and assumptions regarding the rate of nucleotide substitution over time (the molecular clock hypothesis), have allowed researchers to estimate the time of divergence of salmon from these two continents. Nilsson *et al.* (2001) identified 10 substitutions in the 1227 base pair segment of the ND1 gene analyzed, representing DNA sequence divergence of 0.8%, suggesting a time of divergence of greater than 1 million years. Kauppi *et al.* (1997) reported a higher substitution rate (1.8%) in the 940 base pair D loop region analyzed, though D loop sequence is generally more mutable than other regions of the mitochondrial genome in most organisms studied to date.

The existing database of information on mitochondrial and microsatellite DNA variation in Atlantic salmon from within North America and Europe is becoming increasingly comprehensive. This is a result of advancements in technology that permit analyses of additional samples from a greater number of locations and because data from different studies continue to accrue over time; both types of molecular markers have been in use for over 15 years, and are still the primary molecular genetic markers employed today. Despite the large number of loci surveyed, and the thousands of samples analyzed, the above pattern of continent-specific microsatellite and mitochondrial DNA variation still largely holds today. However, over a very small portion of the species range in Europe and North America a percentage of salmon can exhibit mitochondrial and nuclear alleles typical of populations from the alternate continent. For example, European "type" mitochondrial and nuclear microsatellite alleles have been observed in salmon from rivers in Labrador and Newfoundland (King *et al.*, 2000; King *et al.*, 2001; Gilbey *et al.*, 2005). It should be noted, however, that the mitochondrial variant observed in Newfoundland salmon is actually intermediate between the common North American and European types (King *et al.*, 2000). Also, North American "type" microsatellite and mitochondrial DNA variants have been observed in Pecha of northern Russia (Gilbey *et al.*, 2005), albeit at low frequencies. These disjunct distributions of mitochondrial and nuclear variants in the two

continents likely represent limited low-level gene flow between several North American and European populations during early colonization of the species' modern range following retreat of the Pleistocene ice sheet (Knox *et al.*, 2002; Gilbey *et al.*, 2005). Still, overall patterns of variation observed at the mitochondrial ND1 and D loop regions indicate that salmon from these two continents have been largely reproductively isolated for a very long time, probably throughout the last four ice ages.

Neutral molecular genetic variation among North American Atlantic salmon

A well-known characteristic of Atlantic salmon is that mature adults often return to their natal streams to spawn (recently reviewed in Hendry *et al.*, 2004). This, and the possibility of reduced spawning success and lower offspring survival in non-native habitat, contribute to the genetic isolation among neighbouring groups of salmon. But some salmon do stray, spawn successfully, and produce offspring that are capable of surviving to spawn in later years. Analyses of molecular genetic variation can help determine the extent of reproductive isolation among salmon from different locations, at various geographic scales, and hence the potential for adaptive differences to accrue (Waples, 1991). Analyses of molecular genetic variation can also help identify highly divergent lineages that may have accumulated substantial genetic differences over long periods of reproductive isolation (Utter *et al.*, 1993).

Several analyses of genetic variation, involving different types of molecular markers, have been carried out that include salmon from one or more rivers in eastern Canada (Table 1). Most consist of sample collections from several rivers from one or two regions, and a few include collections from one or two rivers from several or all regions. Assessment of heterogeneity among samples within rivers was not a focus of the published studies from Table 1, but was considered by Verspoor (2005). Within-river heterogeneity was not observed among multiple samples collected from four of five rivers; significant differences were only observed between distant tributaries of the very large Saint John River system (Verspoor, 2005).

Surprisingly, few studies actually tested for significant differences between collections from neighbouring rivers, either. Verspoor (2005) reported that "variation among loci was highly heterogeneous at all polymorphic loci, $P<0.00001$)", but did not provide information on specific pairwise comparisons. King *et al.* (2001), in a hierarchical gene diversity analysis, partitioned variance among provinces or states, among rivers within provinces or states, and within rivers; only 2.99% of the variance was associated with among-river comparisons (within province/state), as opposed to 5.28% among rivers within countries in Europe. Pairwise tests for significant differences among populations (rivers) were not provided. McConnell *et al.* (1997) used bootstrap analyses to test for pairwise differences among sample collections from different rivers for three measures of genetic distance: Roger's modified genetic distance, allele sharing genetic distance, and Goldstein's $(\delta\mu)_2$ distance; significant differences were observed for all pairwise estimates of Roger's distance, nearly all estimates of allele sharing genetic distances, but very few estimates of Goldstein's $(\delta\mu)_2$ distance, most of which involved the Gander River, Newfoundland.

A single study of molecular genetic variation involving multiple rivers from all four DFO regions (Newfoundland/Labrador, Quebec, Gulf, and Maritimes) has recently been completed (Verspoor, 2005). In this study, variation was analyzed at 23 allozyme loci, of which 9 were informative (genetically variable). Multi-dimensional scaling analyses and construction of nearest-neighbour joining trees, both based on Nei's D_A distance, indicated to the author the presence of six large-scale groupings of Atlantic salmon in Eastern Canada: Labrador/Ungava, Gulf of Saint Lawrence, Newfoundland (excluding Gulf rivers), Atlantic shore/Southern Uplands

of Nova Scotia, inner Bay of Fundy (iBoF), and outer Bay of Fundy (oBoF) Canada (Figures 1 and 2). Many of the groupings suggested are clearly evident: Labrador and Ungava rivers clearly group together and are distinct from all other samples analyzed, as are salmon from Newfoundland rivers, excluding those that drain into the Gulf of Saint Lawrence (Figure 2). Generally speaking, salmon from the Atlantic coast of Nova Scotia/Southern Uplands cluster together and are distinct from all other samples analyzed (Figure 2), as are salmon from the inner Bay of Fundy. Samples from the Gulf of Saint Lawrence and the west coast of Nova Scotia group together, but are not obviously different from many outer Bay of Fundy populations (Figure 2).

Many of the regional groupings identified above have also been reported in other studies, involving different molecular markers. Verspoor *et al.* (2002) identified a lineage of mitochondrial DNA in multiple inner Bay rivers at moderate-to-high frequency, that is completely absent in outer Bay of Fundy samples surveyed. In a recently expanded, though not yet published, analysis of mitochondrial DNA in Atlantic salmon from Eastern Canada, Verspoor also noted the complete absence of the inner Bay of Fundy mitochondrial DNA lineage in the 16 rivers of the Southern Uplands (Figure 3). In this same study, Verspoor identified a mitochondrial DNA haplotype in nearly all Southern Uplands rivers surveyed that is also absent in the Bay of Fundy and all salmon elsewhere in Eastern Canada (Figure 3). Similarly, measures of differentiation (Nei's 1978 standardized distance, Nei's D_A distance, and F_{ST}) based on analyses of nine microsatellite loci are also generally lower between pairs of rivers within either the inner Bay of Fundy or Southern Uplands areas than between pairs of rivers from these two locations (O'Reilly, unpublished data). Similarly, Spidle *et al.* (2003) and King *et al.* (2001), when attempting to resolve differences among Maine salmon using overlapping suites of microsatellite variation, found that the few inner Bay of Fundy and Southern Uplands populations analyzed were highly distinct from all other populations. In the UPGMA network of microsatellite-based pairwise estimates of Roger's genetic distance published in McConnell *et al.* (1997), the 10 Southern Uplands populations all clustered together, as did the Stewiacke and St. Croix Wells populations (two inner Bay of Fundy populations); the Gaspereau sample again groups separately from all other clades, a likely result of a population bottleneck and rapid, recent genetic drift. The minimal difference reported by King *et al.* (2000) between inner and outer Bay of Fundy populations at the mitochondrial sites surveyed simply reflects the lack of phylogeographically informative sites surveyed compared to the mitochondrial DNA survey of Verspoor *et al.* (2002). The phylogenetic grouping of iBoF and oBoF populations was not evident in the microsatellite survey of Fraser *et al.* (2007). Sample sizes were very small, however, (as low as a few dozen individuals) and the number of loci surveyed (five) was limited.

Evidence also exists for the distinctiveness of Newfoundland populations relative to other North American salmon at microsatellite (Spidle *et al.* 2003; King *et al.*, 2001) and mitochondrial DNA (King *et al.*, 2000), though differences found in the latter study may largely reflect the presence of haplotypes intermediate between North American and European salmon found in east coast Newfoundland samples. Very few studies included samples from Labrador, and even fewer surveyed rivers from Ungava (but see Fontaine *et al.* 1997). King *et al.* (2001) and Spidle *et al.* (2003), in analyses of largely overlapping microsatellite loci, identified the Labrador populations surveyed as highly distinct from other populations.

Overlap or similarity observed between samples from the Gulf of Saint Lawrence and the outer Bay of Fundy by Verspoor (2005) for allozyme loci was also noted by King *et al.* (2001) and Spidle *et al.* (2003) for microsatellite markers. It would be interesting to see whether Gulf and outer Bay of Fundy salmon also exhibit similar mitochondrial DNA haplotype frequencies.

IDENTIFICATION OF UNITS OF CONSERVATION

Introduction and background

Recent acceleration in the global loss of biodiversity, including the extinction of species but also the extirpation of populations, and recognition of the importance of identifying entities for conservation below the species level have resulted in considerable recent efforts to define and refine methods of identifying biological units for conservation. A brief discussion of salient aspects of these approaches are given here (see also Table 2) so that the reader will have this information readily available for assessing later recommendations. More thorough reviews of these approaches can be found in Fraser and Bernatchez (2001) and Ford (2004).

Ryder (1986) first suggested the Evolutionary Significant Unit (ESU), defined as "a subset of the more inclusive entity species, which possess genetic attributes significant for the present and future of the species in question". However, he did not provide much guidance as to how, operationally, such groups should be identified.

Alternate existing methods for identifying units for conservation

Waples (1991) first outlined procedures for the identification of ESUs (termed Distinct Population Segment in his paper) for Pacific salmon under the Endangered Species Act. Under this approach, a group of individuals were designated with ESU status if (1) they were shown to be substantially reproductively isolated from other such groups and (2) represented an important component of the evolutionary legacy of a species. One of the main criticisms of this strategy is that determining whether a group represents an "important component of the evolutionary legacy of the species" is somewhat subjective (see Table 2 for additional information). Another very prominent approach, also already in use in identifying ESUs in some counties, is that of Moritz (1994), which considers a population, or group of populations, to be divergent enough to warrant ESU status when their mitochondrial DNA lineages exhibit reciprocal monophyly (when one group exhibits a mtDNA variant not observed in the other, and vice versa) plus significant differences in allele frequencies at nuclear loci. Although probably the least subjective of the methods discussed, its primary limitations are that 1) it may be too stringent, 2) it does not directly consider adaptive differences, and 3) it does not make use of additional types of information (Table 2).

The method of Crandall *et al.* (2000) for identifying ESUs has garnered increasing interest in recent years, and emphasizes adaptive differences. They advocate an approach based on the degree of ecological and genetic exchangeability (Table 2) using ecological (preferably heritable trait information) and genetic (molecular genetic marker data) information. In addition, a distinction between historic and recent ecological and genetic exchangeability is made. The multiple criteria (historic and recent, ecological and genetic) lend themselves to a graduated system, providing information on the extent of distinctiveness, as opposed to other dichotomous approaches (ESU or not). In their scheme, maximum points for distinctiveness are given to groups that have been ecologically and genetically distinct historically and recently.

Dizon *et al.* (1992), in an approach adapted from Avise (1989), similarly use a graduated method of identifying conservation units (termed "stocks" in their paper), employing distributional, population response, phenotypic and genotypic data as proxies for "total genetic variability for adaptation". Potential CUs are assigned to one of four categories based on (1) the amount of gene flow and (2) likely selection differentials. Their approach differs from others

(including Waples (1991)) in that population response, phenotypic, and genotypic information factor into assessment of selection differential (and likelihood of adaptive differences existing) while distribution data weigh into estimates of gene flow; molecular genetic information does not appear to be used in assessing gene flow. Populations exhibiting little-to-no gene flow and substantial genetic differences are assigned to category 1 (of 4) and represent the most convincing cases for distinctive CU status. The authors emphasize that "meaningful distinctiveness must come from the expression of multiple, independent genetically based traits", as in Avise and Ball (1990).

Utter *et al.* (1993) also utilize molecular genetic and ecological information in identifying ESUs, but in a slightly different way. First, molecular genetic information, supplemented with meristic data, are used to identify major lineages of salmon, and then life history and ecological information are used to identify "the smallest detectable populations with unique sets of characters (i.e. a 'species' under the phylogenetic species concept)" within these major lineages. These units are adaptively distinct populations, equivalent to ESUs identified in some approaches discussed above.

Green (2005) discusses the pragmatic approach to identifying conservation units which he indicates is to be used by the Committee On the Status of Endangered Wildlife In Canada (COSEWIC). In identifying conservation units (termed Designatable Units in his paper), when assessing a pair of candidate groups, the process relies on taxonomic, genetic, and distribution information to evaluate distinctiveness only if the candidates have different extinction probabilities; if the two adjacent groups exhibit similar conservation status, they are grouped as a single unit of conservation.

Identification of ESUs is an intensely debated subject (Pennok and Dimmick, 1997; Waples, 1998), not only because of the different conceptual underpinnings of the various approaches devised to designate populations as distinct, but also because some of these approaches can produce different outcomes in terms of population designation (Fraser and Bernatchez, 2001). Rather than seeing these differences as problematic and impediments to protecting biodiversity, it may be useful to attempt to understand the nature of these differences, and consider the perspective that some of this variation may be put to good use in helping to identify ESUs in Atlantic salmon.

First, some of the variation in methodology and likely outcomes in assigning conservation status reflect the different objectives under which the approaches were conceived and developed (Ford, 2004). For example, the approach described in Green (2005) was developed with the sole intent of listing CUs. If two potentially distinct neighbouring groups of populations under consideration for CU designation have similar conservation status (demographic trajectories or probabilities of extinction), then the mandate of identifying populations for listing can be met by combining both and listing all as endangered, threatened, etc.; why spend limited resources assessing whether or not the two are distinct? In the approach discussed by Green (2005), only when conservation status (extinction probability) differs is there an effort to determine whether the two groups are genetically and adaptively different. If, however, the mandate is to (1) identify all of the distinct "at risk" populations for a database or national inventory and/or (2) assist with the management of declining populations within a given jurisdiction, this approach would not be appropriate.

Second, in many instances, different outcomes produced by different approaches as discussed in the literature (e.g., Fraser and Bernatchez, 2001) involve the comparisons of the prominent methods (i.e. Waples, 1991; Moritz, 1994). The latter is clearly conceptually and

operationally distinct among the methods developed, in that it relies exclusively on molecular genetic differences (principally reciprocal monophyly), which reflects strong long-term reproductive isolation, and does not take into consideration non-molecular genetic information. The conceptual and operational gulf between many of the remaining approaches for identifying ESUs is modest. Ford (2004) also noted that much of the ESU debate appears to be about terminology and language.

Third, as indicated by Fraser and Bernatchez (2001), given the biological complexities involved, it is unlikely that any one approach will be preferable in all instances. In their paper, the authors give examples of how the methods of Waples (1991) and Moritz (1994) give opposite results in two test cases discussed. In one test case, procedures outlined in Moritz's (1994) approach resulted in the failure to list, while procedures followed in Waple's (1991) approach resulted in CU designation; in the other test case, Waple's (1991) approach failed to list while Moritz (1994) identified the candidate group of populations as distinct. The authors then convincingly argue that both groups of populations discussed in the two test cases (all real-world examples) do indeed probably warrant CU status. Clearly, it could be beneficial to employ several different methods (particularly when the exercise represents minimal additional effort), and to look for either concordance or divergence. In instances of the former, the managers would be increasingly confident that their assessment is sound, and in the latter additional insight may be gained by investigating the reason for the different outcomes. Where ambiguity remains, the manager may be guided by the growing consensus that approaches for designating ESUs should (1) utilize multiple data sources and (2) consider, above all, maintenance of adaptive differences and evolutionary processes. This is not to say, however, that ancestral lineages are unimportant. Existing genetic variation created by past evolutionary events is the "reservoir upon which future evolutionary potential depends" (Waples, 1991).

Conservation Units among Atlantic salmon in Eastern Canada: a beginning

It is not the intent of this document to delineate Conservation Units of Atlantic salmon in Eastern Canada, but rather to start the ball rolling by (1) clearly stating the objective of the CU delineation process to be used in the final CSR document, (2) developing a process for systematically identifying candidate populations in Eastern Canada, (3) providing a list of information or data to be collected from candidate populations with which CU status may be evaluated, and (4) developing a method, based on existing published approaches, for evaluating candidate populations for distinct CU status.

The objective of the process used to designate Conservation Units in the Conservation Status Report is to rigorously and systematically assess the degree of 'distinctiveness' of *all* (not just those with different probabilities of extinction) candidate populations of Atlantic salmon in Eastern Canada, where 'distinctiveness' reflects the presence of ancestral lineages and, more importantly, the existence of genetically based adaptive differences.

One approach in cataloguing candidate populations is to list all anadromous salmon runs in Canada by river or major stream of origin, and all land-locked 'populations', as in Table 3. Cryptic sympatric populations, or the presence of multiple allopatric populations within a particular river or lake, can be listed below the first candidate population for that water body. The most comprehensive list of possible cryptic sympatric or within-river allopatric populations can be produced by conducting a thorough review of the available literature, and consulting Federal and Provincial biologists from appropriate departments, authorities from nearby universities and museums, aboriginal groups from the area of concern, and relevant nongovernment organizations, including the Atlantic Salmon Federation and nearby river

associations.

A wide range of information has been used to identify ESUs in the literature reviewed above. Table 4 lists these data types, and will serve to prompt managers to check for the presence of such information. This table could also help to evaluate CU status of populations using some of the more prominent approaches discussed above.

Once the candidate populations have been identified (Table 3) and the appropriate information collected (Table 4), the process of delineating CUs among Canadian Atlantic salmon can begin. Guidelines for identifying ESUs provided by the authors of the various approaches available (Table 2) could be used to complete Table 4, using the data collected. As mentioned previously, many of the different approaches for identifying CUs use similar data to evaluate two broad criteria, reproductive isolation and adaptive divergence. However, approaches may differ in (1) whether the data are used to produce a dichotomous (yes or no) or gradient type response for each criteria type and/or final designation, (2) whether they have an explicit time component for each criteria type (historic versus recent), and 3) which criteria type (reproductive isolation and adaptive divergence) the particular data item addresses. For example, molecular genetic data address only the "Reproductive isolation" criteria in most approaches, but weigh into both broad criteria types in the Waples (1991) approach, and only the "Adaptive divergence" criteria in Dizon *et al.* (1992). This variable use of data by the different methods can be addressed through the following measures. First, for each information or data type required for a CU delineation process, evidence relating to a given criteria could be recorded as a gradient variable (**S**trong (**S**), **M**oderate (**M**), **W**eak (**W**), or Data **U**navailable (**U**)); classes could be combined when fewer, more general groupings are specified by a given procedure. Second, when data are available for recent and historic criteria categories, it can be included in the table, and either used separately or combined (historic plus recent) depending on the requirements of the specific approach. Third, in instances where a given information type is used to address different criteria in different CU designation approaches (molecular genetic marker information as applied in Dizon *et al.* (1992) versus Crandall *et al.* (2000), for example), the author's guidelines can be used to summarize (count or not count) data from information types for a given criterion (column). Once this information has been summarized for each approach at the bottom of the table, decisions based on whether the candidate population is distinct from another can be recorded for a given method that utilizes dichotomous findings (yes or no), and the degree of distinctiveness utilized for others (Dizon *et al.*,1992; Crandall *et al.*, 2000). Results from the various methods can be compared and, together with consideration as to the reason for existing differences, used to reach an overall CU designation or conclusion.

KNOWLEDGE GAPS AND RECOMMENDED FUTURE RESEARCH

In the recent review by Garcia de Leaniz *et al.* (2007b), 97 published studies addressing the existence and magnitude of heritable variation in fitness-related phenotypic traits within and among populations of Atlantic salmon were listed, but very few involved salmon from Eastern Canada. Given the importance of adaptive genetic variation in identifying CUs, additional analyses of whether observed phenotypic variation among Canadian populations are heritable, and whether such differences are adaptive, are sorely needed. As discussed earlier, although there exist several published studies of molecular genetic variation that include salmon from Eastern Canada, most involve one or two populations from several regions, and are of limited scope (e.g., they include analyses of a very small number of informative loci). Extensive mitochondrial ND1 DNA sequence information and analyses have been published for salmon from Maine and the Bay of Fundy area of New Brunswick and Nova Scotia on a fine

geographic scale (Verspoor *et al.* 2002), and some results have been made available for multiple populations from more northern areas of Canada (Verspoor, unpublished reports). Publication of the remaining dataset, including the many rivers of Cape Breton, Newfoundland, Labrador, Ontario and Quebec, would be useful and is encouraged. Data from a large number of microsatellite loci (>10) have also already been acquired for 2,775 anadromous salmon, representing some 51 populations, from the Gulf of Saint Lawrence, northern Quebec, and Ungava (Dionne and Bernatchez, pers. comm.). Acquisition of data from a largely overlapping set of microsatellite loci from over 3,300 anadromous salmon, representing some 31 populations from Nova Scotia and New Brunswick, is also nearly complete (O'Reilly, unpublished data), and microsatellite allele size determinations have already been standardized across the relevant laboratories for 10 microsatellite loci (P. O'Reilly, M. Dionne and L. Bernatchez, unpublished data). Required are 1) additional fine-scale analyses of Newfoundland populations at these same loci (and standardization of microsatellite allele size determinations across relevant laboratories) and 2) summarization and analyses of patterns and extent of genetic variation across the species range in Eastern Canada. Efforts are currently being made to acquire genotype data from these same microsatellite loci from multiple Newfoundland rivers (A. Mansour, DFO Newfoundland, pers. comm.).

Extensive molecular genetic data also exist for MHC II ßI, a locus involved in selfrecognition and immunological responses to pathogens, and for which variation is associated with differential survival of Atlantic salmon to specific virulent pathogens (Langefors *et al.*, 2001). Dionne *et al.* (2007) have recently completed a survey of variation at this locus in over 1,500 individuals from 34 rivers from the Gulf of Saint Lawrence, Labrador, and northern Quebec. Acquisition of data from this important locus from salmon from the Maritimes has been initiated, and it is recommended that a similar survey be carried out among populations from Newfoundland. As all the above marker types exhibit different rates and mechanisms of mutation, and are likely differentially effected by drift and selection, comparison and contrast of variation among marker types across the species range in Canada may help assess levels and patterns of historical and recent gene flow, and the relative effects of drift versus selection in partitioning observed variation among salmon from Eastern Canada.

Finally, although the present document summarizes much of the available molecular genetic information on Atlantic salmon from Eastern Canada, a thorough and comprehensive compilation of ecological variation among rivers and phenotypic differences among populations is urgently required, as is a summary of what is known about movement of individuals among populations. It is hoped that once this is complete, additional information from other classes of molecular markers will be available, as could additional information on heritable variation in important life history characteristics in salmon from some populations from Eastern Canada (D. Fraser, pers. comm.). Also, consensus should be sought from representatives from the different regions from DFO, universities, and NGOs on an approach for identifying CUs. Then, a rigorous and systematic identification of CUs should be possible, where the same (or similar) criteria would be applied across Eastern Canada. The need and benefit of re-assessing CUs should be investigated every 5 to 10 years, and could be warranted if additional information becomes available, or if new and potentially improved methods of identifying CUs are developed.

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Table 1. Summary of analyses of molecular genetic markers in Atlantic salmon from Eastern Canada

Region	Number of populations	Number of loci	Marker type	Sample distribution	Summary of findings
M,G,Q,N, L	11	11	Mi	Course	NFLD highly distinct, Labrador highly distinct, SU highly distinct, Quebec hi distinct, iBoF highly distinct; minimal differentiation between oBoF and Gul
M,G,Q,N, L	22	1	Al	Course	NFLD and Labrador similar and distin Gulf and NS; NS + Maine+Gulf simila
M,G,Q,N, L	10	12	Mi	Course	NFLD highly distinct, Labrador highly distinct, SU highly distinct, iBoF highl distinct; minimal differentiation betwe oBoF and Quebec Note: this is a similar dataset as that u Spidle *et al.* (2003)
M, N	13	8	Mi	Course	Ten SU populations grouped together separate from all others; individual iB highly divergent, but group together b clustering with others; NFLD groups v Gulf
M	46	1	Mt	Fine	iBoF divergent from oBoF and from S SU distinct from NFLD and Gulf (presentation of data not designed to differences among remaining regions
M,G,Q,N, L	53	23	Al	Fine	Six regional groupings suggested by a including 1) Labrador/Ungava, 2) Gulf Saint Lawrence, 3) Newfoundland (ex Gulf), 4) Atlantic shore/SU, 5) iBoF, 6 NFLD and Labrador highly distinct fro others; East Coast NFLD cluster toge and distinct from others (EU influence Gulf similar to oBoF, iBoF distinct, SU

Region	Number of populations	Number of loci	Marker type	Sample distribution	Summary of findings
M	10	1	Mt	Fine	iBoF distinct from oBoF Note: subset of data from Verspoor unpublished
M, N	7	1	Mt	Course	Minimal difference between oBoF and and SU; NFLD distinct because of the presence of haplotypes intermediate between NA and EU in some east co populations
Q,L	7	5	Mi	Course	Some Quebec populations more differentiated from other adjacent populations than from the Ungava po
M	20	9	Mi	Fine	oBoF and iBoF similar; iBoF highly di from SU
M	6	5	Mi	Fine	iBoF populations did not cluster toget distinct from the single oBoF populati surveyed
G,Q,L	34	1	MHC	Fine	Little specific information given on the geographic partitioning of MHC variat temperature-related latitudinal clinal v suggests large-scale population struc and local adaptation at this locus
M,G,Q,L	>50	8-14	Mi, MHC?	Fine	Incomplete

M=Maritimes; G=Gulf; Q=Quebec, N=NFLD; L=Labrador + Ungava
Mi=Microsatellite; Al=Allozyme; mt=Mitochondrial DNA; MHC=Major Histocompatibility Locus
iBoF=inner Bay of Fundy; oBoF=Outer Bay of Fundy; SU=Southern Uplands; NS=Nova Scotia; NA=N

Table 2. Published strategies for identifying and designating Units of Conservation

Reference*	Unit (Abbr.)	Data type	Objective (focus)	Approach	Strengths
Waples (1991)	Evolutionary Significant Unit **(ESU)** or Designatable Unit **(DU)**	-neu. mol. gen. markers -phenotypic -life history -ecological	-identify units for listing under Endangered Species Act legalisation	-substantial reproductive isolation -important component of evolutionary legacy of species -data types used to address both criteria	-flexible -makes use of m types
Moritz (1994)	Evolutionary Significant Unit **(ESU)**; Management unit **(MU)**	-mtDNA -Nuclear DNA	-identify groups that have experienced long periods of independent evolution (maintain evolutionary heritage)	-Reciprocal monophyly -differentiation at nuclear markers	-non subjective -considers hist. a time frames
Crandall *et al.* (2000)	**None**	-heritable characters (see approach) -neu. mol. gen. markers	-identify distinct population segments (maintenance of adaptive diversity and evolutionary potential) -identify units for management	-test for genetic exchangeability (through neu. mol. gen. markers) (Nm>1)(unique alleles) -overlay ecological exchangeability (through heritable characters like life hist., ecol. requirements, morphological and demographic characteristics on genetic exchangeability) -application of procedure of Templeton and Sing	-considers hist. a diff. evolutionary -gradient of pop. distinctiveness (ε -makes use of m types -less susceptible -more complete u
Dizon *et al.* (1992)	**Stock**	-distrib. + abundance -population response -phenotypic -genotypic (neu. mol. gen. markers and others)	-identify distinct population segments	-estimate magnitude of potential gene flow as inferred from distribution data/abundance etc. -test for existence of multiple genetically based traits or adaptations (demographic, morphological, isozyme, mtDNA)	-gradient of popu distinctiveness (4 phylogeographic -makes use of m types -more complete u SOME available
Vogler and Desalle (1994)	Evolutionary Significant Unit **(ESU)**	-any heritable trait	-identify distinct population segments	-identify group of individuals sharing a unique heritable character	-non-subjective -makes use of m types

Reference*	Unit (Abr.)	Data type	Objective (focus)	Approach	Strengths
Utter *et al.* (1993)	Distinct Population Segment **(DPS)**	-neu. mol. gen. markers -meristic characters -ecological info. -life history info.	-identify distinct population segments	-first identify major genetic lineages using neu. mol. gen. markers and meristics -systematic survey of adaptive differences within groupings within major lineages -identify DPS from above information	-considers hist. a time frames and evolutionary proc -makes use of m types
Green (2005) (COSEWIC)	Designatabl e Unit **(DU)**	-conservation status -taxonomic, molecular genetic -biogeographic	-identify units for listing	-determine extinction probabilities of putative DUs -if similar, group -if different, assess other data types	-practicable -efficient -makes use of m types
SARA	**Species**	-geographic -genetic	-identify units for conservation -management	-examine geographic distribution in Canada -examine genetic information -consider socio-economic implications of listing -decision to list made by the responsible Minister	-practicable -considers social economic criteria

*Reference= Source of additional information; Neu. mol. gen. markers= neutral molecular genetic markers (allozymes, mitochondrial DNA, microsat mitochondrial DNA; Nm=effective number of migrants per generation.

Table 3. Candidate populations of land-locked and anadromus Atlantic salmon *(Salmo salar)* in Eastern Canad status

Population name	Province/ territory	General location (water body)	Specific location (water body)	Latitude	Longitude	Alternate sympat population

Table 4. Data checklist and form to tabulate criteria score for CU designation

	Criteria type			
Information type	Historic reproductive isolation	Present day reproductive isolation	Historic adaptive divergence	Present day adaptive significance
Geographic (distributional data)				
Geographic distance between proposed units				
Geographic disjunction (yes/no)				
Geographic or physical barrier to migration				
Abundance or density information				
Movement/migration observations				
Tagging information				
Telemetry information				
Molecular genetic markers				
Mitochondrial DNA frequency differences (terminal or non-terminal nodes)(recent samples)				
Mitochondrial DNA frequency differences (terminal or non-terminal notes)(historic samples)				
Mitochondrial DNA fixed differences at terminal nodes (Nested Clade Analysis)				
Mitochondrial DNA fixed differences at internal nodes (Nested Clade Analysis)				
Microsatellite DNA (recent samples)				
Minisatellite DNA (historic samples)				
cDNA (recent samples)				
AFLP (historic samples)				

Allozyme (recent samples)				
Malic Acid allozyme locus				
MHC II Beta 1 Exon II				
Others				
Ecological				
Temperature				
Photoperiod				
Stream morphology, substrate and gradient				
Predator type/abundance				
pH				
Marine migration distance				
Prey				
Parasite type/density				
Life History (Dizon *et al.* (1992) population response data)				
Time of hatching				
Years as parr				
Smolt Ocean migration				
Years at sea				
Date enter river				
Date of spawning				
Egg size				
Fecundity				
Proportion mature parr				
Morphology				
Behaviour				
Conservation status (Green)				
Summary of criteria scores by approach				

Waples (1991)				

Moritz (1994)				
Crandall *et al.* (2000)				
Dizon *et al.* (1992)				
Vogler and Desalle (1994)				
Utter *et al.* (1993)				
Green (2005) (COSEWIC)				
SARA				
Approach-specific conclusions				
Waples (1991)				
Moritz (1994)				
Crandall *et al.* (2000)				
Dizon *et al.* (1992)				
Vogler and Desalle (1994)				
Utter *et al.* (1993)				
Green (2005) (COSEWIC)				
SARA				
Information type	Historic reproductive isolation	Present day reproductive isolation	Historic adaptive divergence	Present day adaptive significance
Overall Conclusion				

S=strong evidence for rejecting the Null hypothesis of NO DIFFERENCE between candidate populations
M=moderate evidence for rejecting the Null hypothesis of NO DIFFERENCE between candidate populations
W=weak evidence for rejecting the Null Hypothesis of NO DIFFERENCE between candidate populations
U=unavailable

Figure 1. Map of the location of Canadian rivers sampled for allozyme analysis by Verspoor (2005).

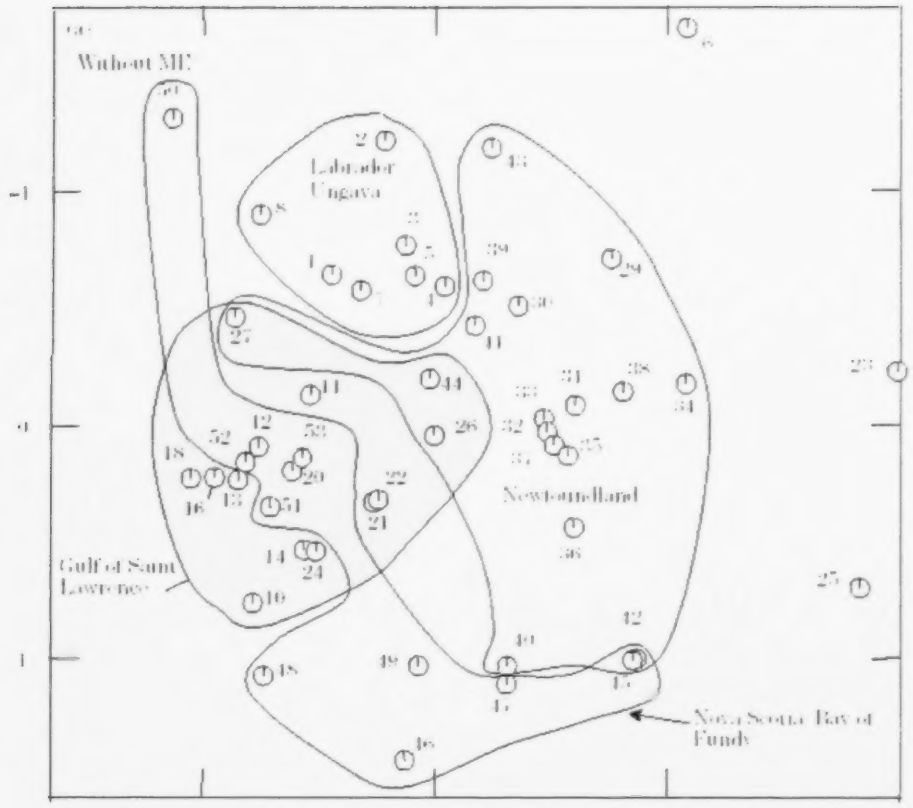

Figure 2. Two-dimensional representation of a Multi-dimensional Scaling (MDS) plot of Canadian Atlantic salmon populations based on Nei's D_A genetic distance (Verspoor, 2005)

Figure 3. Distribution and frequency of mitochondrial DNA haplotypes unique to salmon of the inner Bay of Fundy (black) and Southern Uplands (grey), from Verspoor (unpublished data).

APPENDIX I.

Table A1. Evidence for heritable variation in fitness-related phenotypic traits among and within populations of Atlantic salmon. Asterisks indicated studies suggesting genotype-by-environment interactions. 'Environment' refers to the testing conditions (W, wild releases; L, Laboratory or cage conditions; S, seminatural channel), 'Stage' refers to the freshwater (F) and marine (M) stages of salmon development, and 'Method' refers to the primary approach or method(s) used to detect genetic variation in phenotypic traits (1: comparative ecological correlates; 2: genetic differences among families or populations; 3: translocations/common garden experiments; 4: mark-recapture of individuals with different traits; 5: experimental manipulation of traits; 6: QST method, QTL, genomics, see text). From Garcia de Leaniz *et al.* (2007b).

Dependent trait	Environment	Stage	Method	Reference
Among populations				
Body size*[a]	W	M	2	Jonasson *et al.* (1997)
Body size	L	F	2	Jonasson (1993)
Body Morphology	L	F	1,2	Riddell *et al.* (1981)
Body Morphology	L,S	F	2	Fleming and Einum (1997)
Growth rate	L	F	2	Holm and Ferno (1986)
Growth rate	L	F	2	Nicieza *et al.* (1994b)
Growth rate	L	F	2	Torrissen *et al.* (1993)
Growth rate	W	M	2	Friedland *et al.* (1996)
Growth rate	L,W	F	2,3	McGinnity *et al.* (1997)
Growth rate	L,W	F&M	2,3	McGinnity *et al.* (2003)
Growth rate *[a]	L	M	2	Gunnes and Gjedrem (1978)
Growth rate *[b]	L	F	1,2	Jonsson *et al.* (2001)
Growth rate	L,W	F	2	Einum and Fleming (1997)
Growth rate	L,S	F	2	Fleming and Einum (1997)
Growth efficiency*[b]	L	F	1,2	Jonasson *et al.* (2001)
Muscle growth*[b]	L	F	1,2	Johnston *et al.*, (2000b,c)
Muscle growth	L	F	1,2	Johnston *et al.*, (2000a)
Digestive rate	L	F	2	Nicieza *et al.* (1994a)
Embryo development	L	F	2	Berg and Moen (1999)
Survival	L,W	F	2,3	McGinnity *et al.* (1997)
Survival	L,W	F&M	2,3	McGinnity *et al.* (2003)
Survival	L	F	2	Jonasson (1993)
Survival	W	F&M	2	Garcia de Leaniz *et al.* (1989)
Survival	W	F&M	2	Verspoor and Garcia de Leaniz (1997)
Survival	W	M	1	Friedland *et al.* (1996)
Survival	W	M	3	Hansen and Jonsson (1990)
Survival*[a]	W	M	3	Jonasson (1996)
Survival*[a]	W	M	2	Jonasson *et al.* (1997)
Survival*[c]	L	F	2	Gjedrem and Aulstad (1974)
Survival*[d]	L,W	F	2,3	Donaghy and Verspoor (1997)
Survival*[d]	L	F&M	1,2	Rosseland *et al.* (2001)

Gyrodactylus resistance	L	F	1,2	Bakke *et al.* (1990), Bakke (1991)
Age at sexual maturity	W	M	2,3	McGinnity *et al.* (2003)
Age at sexual maturity	L	M	1,2	Naevdal *et al.* (1978)
Age at sexual maturity	L,W	M	3	Jonasson (1996)
Age at sexual maturity*	L	M	1,2	Glebe and Saunders (1986)
Age at sexual maturity	L	M	2	Holm and Naevdal (1978)
Male parr maturation*	L	F	1,2	Glebe and Saunders (1986)
Marine migrations	W	M	1,2,4	Kallio-Nyberg and Koljonen (1999)
Marine migrations	W	M	1,2,4	Kallio-Nyberg *et al.* (1999)
Smolt migration timing	W	F	2	Aarestrup *et al.* (1999)
Smolt migration timing	W	F	2,3	Nielsen *et al.* (2001)
Smolt migration timing	W	F	2	Orciari and Leonard (1996)
Timing of hatching	L,W	F	2,3	Donaghy and Verspoor (1997)
Seasonal run-timing	W	M	3	Hansen and Jonsson (1991)
Seasonal run-timing	W	M	2,3	Stewart *et al.* (2002)
Sheltering behaviour	L	F	1,2	Valdimarsson *et al.* (2000)
Aggression levels	L	F	1,2	Holm and Ferno (1986)
Aggression levels*	L	F	2,3	Einum and Fleming (1997)
Predator avoidance	L	F	2,3	Einum and Fleming (1997)
Aggression levels*	L,S	F	3	Fleming and Einum (1997)
Predator avoidance	L,S	F	3	Fleming and Einum (1997)
Predator avoidance	L	F	1,2	Jonasson *et al.* (2001)
Within populations				
Body size	L	M	2	Gjedrem (1979)
Body size	L	F	2	Naevdal (1983)
Body size	L	F	2	Friars *et al.* (1990)
Body size	L	F	2	Rye and Refstie (1995)
Body size*	W	F	2	Garant *et al.* (2003)
Body size	W	F	4	Hendry *et al.* (2003)
Condition factor	W	F	4	Hendry *et al.* (2003)
Egg size	S,W	F	4,5	Einum and Fleming (2000a,b)
Egg size	L	F	2	Pakkasmaa *et al.* (2001)
Growth rate	L	F	2	Thorpe and Morgan (1978)
Growth rate	L	F&M	2	Gjerde (1986)
Growth rate	L	F	2	Friars *et al.* (1990)
Growth rate	L	F	2	Rye *et al.* (1990)
Growth rate	L	F	2	Torrissen *et al.* (1993)
Growth rate	L	F	2	Thodesen *et al.* (2001)
Growth rate*	W	F	2,5	Garant *et al.* (2003)
Growth rate	W	F	4	Hendry *et al.* (2003)
Growth efficiency	L	F	2	Thodesen *et al.* (2001)
Feeding rate	L	F	2	Thodesen *et al.* (2001)
Embryo development	L	F	2	Berg and Moen (1999)
Date of emergence	S,W	F	4,5	Einum and Fleming (2000a,b)
Date of emergence	W	F	4	Garcia de Leaniz *et al.* (2000)

Length of emergence	S,W	F	4,5	Einum and Fleming (2000a,b)
Alevin length	W	F	4	Garcia de Leaniz *et al.* (2000)
Marine migrations	W	M	2,4	Kallio-Nyberg *et al.* (2000)
Marine migrations	W	M	2,4	Jutila *et al.* (2003)
Survival	L	F	2	Rye *et al.* (1990)
Survival	L	F	2	Thorpe and Morgan (1978)
Survival*	L	F	2	Fevolden *et al.* (1993,1994)
Survival*	L	F	2	Gjedrem and Gjoen (1995)
Survival*[c]	L	F	2	Langefors *et al.* (2001)
Survival*[c]	L	F	2	Lund *et al.* (1995)
Survival*[c]	L	M	2	Bailey *et al.* (1993)
Survival*[c]	L	M	2	Standal and Gjerde (1987)
Survival*[d]	L	F	2	Schom (1986)
Survival*[e]	L	F	2	Gjoen *et al.* (1997)
Early survival	W	F	4	Garcia de Leaniz *et al.* (2000)
Stress	L	F	2	Fevolden *et al.* (1991)
Sea louse infection*	L	M	2	Mustafa and MacKinnon (1999)
Age at sexual maturity	L	M	2	Naevdal (1983)
Age at sexual maturity	L	M	2	Gjerde (1984)
Age at sexual maturity*	L,W	F	6	Aubin-Horth *et al.* (2005)
Muscle growth	L	F	2	Johnston *et al.* (2000b)
Reproductive success	W	F	2,5	Garant *et al.* (2003)

[a] Differences in relative performance among rearing/release locations.
[b] differences in relative performance among different temperatures.
[c] differences in resistance to diseases.
[d] differences in tolerance to low pH levels.
[e] negative genetic correlation between resistance to viral and bacterial disease.
QTL, quantitative trait loci.
QST method, extent of population differentiation in quantitative traits (Q_{ST}) presumed to be affected by selection relative to neutral molecular markers (F_{ST}).

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